

INFLORESCENCE ARCHITECTURE OF *EUCNIDE* (LOASACEAE)

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ABSTRACT

Terminal inflorescences and axillary flowers have been reported in recent revisions of *Eucnide* (Loasaceae). Developmental studies show, however, that axillary flowers are not present. All flowers are terminal: the initial shoot axis terminates in a flower, and lateral branches that terminate in flowers after producing only one or two leaves arise from the distal nodes of each initial and renewal axis. The branching pattern in the inflorescence region of each axis is complicated by the apparent displacement of subtending leaves outward onto lateral floral branches during their extension. Renewal axes that first arise in the nodes subjacent to lateral floral axes reiterate the pattern of the initial axis.

Recent systematic treatments of *Eucnide* (Loasaceae) have largely underestimated the architecture of the inflorescence. Waterfall (1959) used floral position to separate "two natural, but somewhat intergrading series in the genus." His first series, comprised of *E. bartonioides*, *E. xylinea*, and *E. urens*, was characterized by solitary flowers in leaf axils. The second series had "terminal inflorescences more or less developed." The most recent revision by Thompson and Ernst (1967) distinguished three sections in *Eucnide* (including *Sympetaleia* at the sectional level; Waterfall did not consider *Sympetaleia* to be congeneric with *Eucnide*). Thompson and Ernst did not retain the informal division based on floral position proposed by Waterfall, and inflorescence data does not appear to have had a major role in their sectional circumscriptions. They observed terminal inflorescences of a few flowers in most species and noted axillary flowers in more than half of the species. The only inflorescence data given for the new species *E. durangensis* (Thompson and Powell 1981) was in the Latin description: "*Inflorescence pauci-vel multiflorae*".

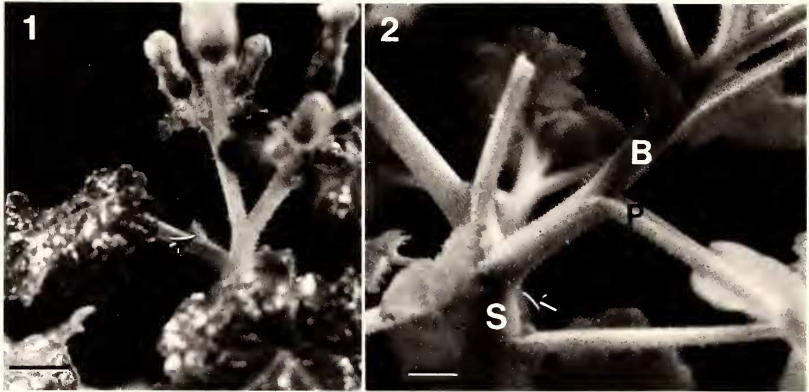
My investigations show that our current knowledge of inflorescence morphology of *Eucnide* is oversimplified. The purpose of this paper is to clarify the inflorescence architecture of *Eucnide* by placing it in the context of whole plant morphology and development.

MATERIALS AND METHODS

Eucnide bartonioides (seven plants), *E. cordata* (four plants), *E. hirta* (two plants), and *E. lobata* (three plants) of Thompson and Ernst's sect. *Eucnide* and *E. aurea* (three plants) of sect. *Sympetaleia*

TABLE 1. PERTINENT COLLECTIONS OF *Eucnide* USED FOR THIS INVESTIGATION.
 * = collections that were sources of seeds for glasshouse populations.

Species	Collection
Sect. <i>Eucnide</i>	
<i>E. bartonioides</i> Zucc.	USA, Texas: Big Bend National Park, 26 Jun 1962, <i>Thompson and Ernst 3283</i> (LA)*. MEX, Tamaulipas: Jaumave, 25 Nov 1962, <i>Moran 10031</i> (LA, UC); Nuevo Leon: Cuesta de Mamiluque, 14 Aug 1942, <i>Gentry 6729</i> (UC).
<i>E. cordata</i> (Kell.) Kell. ex Curran	MEX, Baja California Sur: La Paz, 29 Dec 1958, <i>Porter 106</i> (LA); Sierra de la Gigantea, 9 Nov 1961, <i>Carter 4278</i> (UC); Isla Monserrate, 27 Mar 1977, <i>Cody (Thompson 3829 seed collection)</i> (LA)*.
<i>E. durangensis</i> Thompson & Powell	MEX, Durango: Gomez Palacio, 25 Mar 1973, <i>Johnston, Wendt, and Chiang 10417</i> (LA); Torreon, 14 Aug 1973, <i>Henrickson 12405</i> (LA).
<i>E. floribunda</i> S. Wats.	MEX, Coahuila: Cuatro Ciénegas, 10 Jun 1968, <i>Lehto, Keil, and Pinkava 5360</i> (LA); 4 Apr 1969, <i>LaBounty, Lehto, and Pinkava 5927</i> (LA); Las Delicias, 12 Aug 1973, <i>Henrickson 12240</i> (LA).
<i>E. grandiflora</i> (Groenl.) Rose	MEX, Oaxaca: Tomellin Canyon, 17 May 1894, <i>Pringle 4645</i> (GH); Jayacatlan, 4 Nov 1973, <i>Breedlove 35885</i> (RSA); Teotitlan del Carmen, 22 Aug 1975, <i>Webster, Armbruster, and Holstein 20036</i> (GH).
<i>E. hirta</i> (G. Don) Thomp- son & Ernst	MEX, Jalisco: San Cristobal de la Barranca, 11 Nov 1962, <i>McVaugh 22140</i> (NY, LL); Tizapan, 30 Jun 1957, <i>McVaugh 15108</i> (<i>Thompson 3319 seed collection</i>)*; Veracruz: Cerca de Puente Nacional, 13 Jan 1973, <i>Hernandez, Dorantes, and Dorantes 1819</i> (NY).
<i>E. hypomalaca</i> Standl.	MEX, Chihuahua: Batopilas, 15 Apr 1948, <i>Hewitt 272</i> (GH); Chiapas: Chiapa de Corzo, 24 Feb 1973, <i>Breedlove 33828</i> (RSA).
<i>E. lobata</i> (Hook.) A. Gray	MEX, Hidalgo: Barranca de Toliman, 27 Nov 1962, <i>Moran 10048</i> (LA); Nuevo Leon: Monterrey, 10 Aug 1959, <i>Waterfall 15324</i> (F) (<i>Thompson 3298-6 seed collection</i>) (LA)*; Coahuila: Carmen Pass, 6 Aug 1978, <i>Fryxell 3023</i> (ASU)*.
Sect. <i>Sympetaleia</i>	
<i>E. aurea</i> (A. Gray) Thompson & Ernst	MEX, Baja California: Sierra de la Gigantea, 25 Nov 1953, <i>Carter and Kellogg 3266</i> (UC); Isla Carmen, 10 Mar 1960, <i>Carter and Ferris 3710</i> (UC); Idlefonas Island, 2 Apr 1962, <i>Moran 9056</i> (ASU)*.
<i>E. rupestris</i> (Baill.) Thompson & Ernst	MEX, Baja California: Mexicali, 22 Feb 1960, <i>Raven 14802</i> (LA); San Estaban Island, 22 Mar 1962, <i>Moran 8858</i> (LA); Bahia de Los Angeles, 26 Feb 1963, <i>Thorne and Henrickson 32694</i> (LA).
<i>E. tenella</i> (I. M. Johnst.) Thompson & Ernst	MEX, Baja California Sur: Mission Los Delores, 5 Dec 1951, <i>Wiggins, Carter, and Ernst 260</i> (LA); Sierra de la Gigantea, 31 Oct 1971, <i>Moran 18845</i> (UC); Sierra de la Gigantea, 5 Nov 1971, <i>Moran 19017</i> (UC).
Sect. <i>Mentzeliopsis</i>	
<i>E. urens</i> Parry	USA, California: Whipple Mountains, 20 Mar 1936, <i>Clary 2580</i> (JEPS); near Death Valley National Monument, 17 Mar 1984, <i>Hufford 1114</i> (UC); Trona, 18 Mar 1984, <i>Hufford 1116</i> (UC); MEX, Baja California: Okie Landing, 4 May 1966, <i>Moran 13124</i> (UC).



FIGS. 1-2. Recauscence in *Eucnide*. FIG. 1. Axillary bud (arrow) displaced onto petiole of leaf in *E. aurea*. FIG. 2. After extension of the lateral branch, the subtending leaf (P indicates the petiole of the leaf) appears to be inserted on the lateral branch (B) derived from its axil because of extension of the common basal portion of both leaf and branch. Arrow indicates position of insertion of the leaf (P) on the axis (S) where it arose in *E. cordata*. Scale bars equal 5 mm.

were grown under glasshouse conditions in Berkeley, California. *Eucnide urens*, comprising sect. *Mentzeliopsis*, was examined under natural conditions (Table 1). I examined herbarium specimens of all species, except *E. xylinea* C. H. Muller. Collection data for pertinent herbarium specimens and sources of seeds for glasshouse populations are given in Table 1.

The term inflorescence is used in this paper in the sense of Steenis (1963), who defined it as "the specialized fertile part(s) of an individual plant which post anthesin does (do) not participate in the vegetative extension of the individual", and is hence either shed or withering away."

RESULTS

All species of *Eucnide* are perennial. The shoot system is sympodial; each shoot axis eventually terminates in a flower. A slight concaulescence (adnation of the pedicel of the terminal flower with the uppermost lateral branch, Troll 1964) is common among all of the species, although it is not a consistent feature of all individuals of any species. Plants grown under glasshouse conditions develop approximately five to ten leaves following the cotyledons and before terminal flower formation. The distal-most leaves of each axis are recaulescent (*sensu* Troll 1964, see also Kuijt 1981) with their axillary buds. Recauscence implies that an axillary bud is somewhat displaced onto the petiole of the subtending leaf (Fig. 1; this con-

dition is also called epipetioly, Dickinson 1978). When the axillary bud begins extension the basal region common to the subtending leaf and axillary bud also begins outgrowth. At full extension of a lateral floral branch, the 'subtending leaf' appears to be inserted on the lateral axis rather than on the axis on which it was produced (Fig. 2).

Sect. EUCNIDE. In glasshouse populations of *E. bartonioides*, *E. hirta*, and *E. lobata*, the three leaves and axillary buds subjacent to the terminal flower are recaulescent (Figs. 3, 4). Of these three uppermost nodes, lateral floral axes usually arise in the axils of the two distal leaves (forming a dichasial inflorescence, Figs. 3, 4), although only the uppermost node may form a lateral floral axis (a monochasial inflorescence). The terminal flower and either the monochasial or dichasial lateral floral axes form the inflorescence of each shoot axis. Lateral floral axes in these species do not undergo extensive internodal elongation. Internodes of these lateral floral axes elongate only as flowers begin to mature and then most of the elongation is in the pedicel. Each lateral floral axis usually produces two leaves (Fig. 5) or may form only one leaf (Fig. 6) and a terminal flower. Each leaf of this primary lateral axis becomes recaulescent with the bud in its axil. Each of these axillary buds (secondary lateral axes) repeats this pattern of producing one or two leaves (each becoming recaulescent with its axillary bud) and a terminal flower (Figs. 5, 6). The lateral floral axes may be either dichasial (Fig. 5) or monochasial (Fig. 6). Some herbarium specimens show that inflorescence development changed from one condition to the other during ontogeny. Lateral floral axes were not observed (in neither glasshouse populations nor on herbarium specimens) to convert back to vegetative growth (i.e., back to production of more than two leaves before terminal flower formation). This pattern of inflorescence architecture appears to be common to all species of section *Eucnide* (except *E. xylinea*, which was unavailable, and *E. cordata*, which is discussed below) as ascertainable from examination of herbarium specimens (Table 1).

Leaf form undergoes a gradual transformation in the transition to the flowering region. Leaf laminae with a lobate margin and a cordate base are produced in the vegetative portion of the plant. At the few nodes proximal to the inflorescence region, where the internodes do not extensively elongate, the leaves are smaller. Leaves lose regularly lobed margins and cordate bases with transition into the region of lateral floral axes. Leaves on some primary, secondary, and tertiary axes of the inflorescence often occur as tiny, lanceolate bracts.

The recaulescent 'node' (involving leaf and axillary bud) on the main shoot, which was not immediately floral, is the location of the first renewal shoot (Figs. 3, 4) or innovation shoot (sensu Weberling



FIGS. 3-10. Renewal growth and inflorescence architecture of *Euclide*. FIG. 3. Monochasial renewal, one renewal branch arises from the node proximal to the lateral flowering axes. FIG. 4. Dichasial renewal, vegetative branches arise from the two nodes proximal to the lateral flowering axes. FIG. 5. Flower and leaf positions on dichasial floral axes that would be located at positions indicated by solid arrows in Figs. 3 and 4. Terminal flowers of successive lateral axes are indicated. FIG. 6. Flower and leaf positions on monochasial floral axes that would be located at positions indicated by solid arrows in Figs. 3 and 4. Terminal flowers of successive lateral axes are indicated. FIG. 7. Shoot terminus of *E. cordata* prior to secondary branching of the inflorescence. FIG. 8. Architecture of *E. cordata* inflorescence. Terminal flowers of primary, secondary, and tertiary axes are indicated for one of the three floral branches. FIG. 9. Architecture of shoot system of *E. tenella*, showing dichasial branching on left side and monochasial branching on right. FIG. 10. Architecture of inflorescence of *E. urens*, showing displacement (concaulescence) of terminal flowers toward subjacent lateral branches. A = terminal flower, B = floral branch, C = vegetative branch, D = leaf produced by axis on which it is inserted, E = leaf produced by axis

1983). The subjacent node at which there is usually no recaulescence has an axillary bud that subsequently begins renewal growth. The sympodial growth pattern appears to be primarily, although not strictly, dichasial (Fig. 4). Monochasial renewal (Fig. 3; especially in *E. lobata*) and also pleiochasial renewal growth (usually three branches in *E. bartonioides*) are common. Following transition to flowering on a renewal axis, buds in leaf axils (although these leaves have withered) of the previous axis also will begin growth. Outgrowth of buds along this axis is basitonic (i.e., beginning near the base of an axis with acropetal progression). The first few internodes of renewal axes elongate. As an axis nears flowering, internodes remain largely unextended. Each renewal shoot produces only five to ten leaves before forming a terminal flower. The inflorescence of any shoot axis in *Eucnide* may be considered to be the region above the uppermost renewal branch because this portion of the plant usually dries and withers after flowering (it does not contribute to further vegetative extension). Renewal growth patterns were difficult to determine for species that were not grown under glasshouse conditions because herbarium specimens seldom have enough of the plant for evaluation.

Eucnide cordata differs from all species described above. It has longer renewal shoots that produce more leaves before conversion to flowering. The internode, between the lowest node with a leaf that becomes recaulescent and a nonrecaulescent leaf, becomes elongated when flowering begins. The next distal internode also becomes quite elongated and effectively segregates an inflorescence region that is more distinct than in the other species of sect. *Eucnide*. These penultimate internodes in the other species remain compact.

The basic architectural pattern of the flowering region in *E. cordata* is similar to that described above for other species in sect. *Eucnide*; however, there are some distinctions. Three lateral floral axes (Fig. 7) are produced on the initial axis and each renewal branch, rather than the two most commonly produced in *Eucnide* (Figs. 3, 4). Each of these primary lateral axes (Fig. 8) produces two or occasionally more leaves and a terminal flower. The leaf subtending a primary lateral axis becomes recaulescent as is common in *Eucnide*. The first leaf produced by a primary floral axis often remains at nearly the same level as the subtending leaf because the internode between them does not elongate. An axillary bud may or may not form in association with this first leaf. If an axillary bud does form it is floral

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subjacent to the one on which it is inserted (recaulescence). T = terminal flower, 1° = flower of primary, 2° = flower of secondary, 3° = flower of tertiary, and 4° = flower of quaternary floral branches.

(a secondary floral axis). This secondary floral axis produces two leaves, but only the uppermost produces an axillary bud that is floral (a tertiary lateral axis). The uppermost leaf of the primary lateral axis also has an axillary bud. This again becomes a secondary floral axis that produces two leaves, only one of which subtends a floral bud (another tertiary lateral axis). Each tertiary axis present (there may be two associated with each primary lateral axis) produces two leaves (one of which has an axillary bud) and a flower. Leaves on these floral axes, which subtend axillary buds, usually become recaulescent with that lateral axis when the axis begins growth. The lateral axes in the inflorescence region of *E. cordata* have greater internodal growth than is common among the other species of sect. *Eucnide*.

Renewal growth in *E. cordata* is dichasial. Renewal branches arise in the axils of two leaves subjacent to the floral nodes. It is usually below the region where extensive internodal elongation occurred concurrent with flowering. Each renewal axis may or may not be recaulescent with its subtending leaf.

Sect. SYMPETALEIA. *Eucnide aurea* and *E. rupestris* have an inflorescence pattern similar to that identified as the most common among the species of sect. *Eucnide*. Each lateral floral axis of *E. aurea* and *E. rupestris*, examined on herbarium specimens, may be monochasial (Fig. 6) or dichasial (Fig. 5) (as also was true of most species of sect. *Eucnide*). *Eucnide tenella* (Fig. 9), unlike these other species of sect. *Sympetaleia*, lacks distinct lateral floral branches and renewal branches. Axes (Fig. 9; initial axes were unavailable on herbarium specimens) produce either one or two leaves and a terminal flower. Each leaf of an axis usually is recaulescent with its axillary bud. Each of these axillary buds reiterates the pattern of producing one or two leaves (each of which usually will be recaulescent with its axillary bud) and a terminal flower.

Unlike the other species grown under glasshouse conditions, *E. aurea* is likely to have up to six flowers that open concurrently on a single renewal axis. In the other species, usually only one or two flowers associated with any one renewal axis were observed to be open concurrently. The internodes of the lateral floral axes of *E. aurea* also elongate to a greater extent over the period of flowering than do the corresponding internodes in most species of sect. *Eucnide*.

Renewal growth in *E. aurea* appears to be primarily monochasial (Fig. 3). As in the other species, the primary renewal axis is one of the recaulescent axillary buds subjacent to the terminal flower. Other reiterative lateral shoots with a vegetative phase (i.e., producing more than two leaves before forming a terminal flower) begin growth after the renewal shoots from an axis have begun to flower. Renewal

growth of *E. rupestris* was impossible to determine from herbarium specimens.

Sect. MENTZELIOPSIS. *Eucnide urens* (Fig. 10) is distinct in having terminal flowers displaced from the notch between the two subjacent lateral flowering axes. In some of the other species, the terminal flowers of vegetative axes are sometimes somewhat confluent with the uppermost lateral axis that is flowering (concaulescence, sensu Troll 1964). The actual developmental process that causes this displacement in *E. urens* is unclear, although it also appears to be concaulescence. The lateral floral shoots in *E. urens* (Fig. 6) largely are the same as in most species of sect. *Eucnide*, except for the distinctive terminal flower displacement. *Eucnide urens* also differs from the species in sects. *Eucnide* and *Sympetaleia* because the leaf directly beneath a terminal flower is clasping. Renewal growth data for *E. urens* is unavailable because I could not obtain adequate growth of this species in glasshouse populations.

DISCUSSION

Eucnide has monotelic axes (sensu Troll 1964) because each shoot terminates in a flower. Troll (1964) suggested that the Loasaceae is among a group of families characterized by monotelic synflorescences (i.e., monotelic shoots associated with the initial and each renewal axis).

Inflorescences in *Eucnide* were first described as cymes (Urban 1886). Urban (1892) later described inflorescence patterns in various loasaceous species, including *E. bartonioides*. For *E. bartonioides*, he described two or three floral branches beneath the terminal flower. Each floral branch was observed to be adnate with its subtending leaf and to produce two prophylls before terminating in a flower. Each prophyll subtended a similar branch and was likewise adnate with it. His set of observations concur with the patterns I have described for *E. bartonioides*, and generally characterize the patterns found among most of the species (*E. cordata*, *E. tenella*, and *E. urens* are divergent the most notably).

No major distinctions in inflorescence architecture seem to differentiate sect. *Sympetaleia* from sect. *Eucnide*. Within both sections there are variations (*E. cordata* in sect. *Eucnide* and *E. tenella* in sect. *Sympetaleia*) from the commonly expressed patterns. Gilg (1925) described *Eucnide* as having flowers arranged in cymes (presumably implying dichasia in this instance) and monochasia. He described the genus *Sympetaleia* (synonymized with *Eucnide* by Thompson and Ernst, although they segregated these species into sect. *Sympetaleia*) as having flowers arranged in few-flowered cymes. Gilg's use of the term cyme appears to imply a dichasial branching pattern

in the inflorescence, and this concurs with my observations of dichasial inflorescences in *E. aurea* and *E. rupestris*. Although the initial and renewal axes tend to form two lateral floral axes (dichasia) in *E. aurea* and *E. rupestris*, I have observed that the successive iterations of floral branches from each of these lateral floral axes may be either dichasial or monochasial.

Eucnide tenella is the only species of *Eucnide* that probably should not be considered to have either a monochasial or dichasial cyme. This species was described (Johnston 1924) only a year before Gilg (1925) published descriptions of *Eucnide* and *Sympetaleia*, and *E. tenella* was not included among them. The growth pattern of *E. tenella* appears to be a simplification of that found in the other species of *Eucnide* because it has neither distinct lateral floral branches nor distinct renewal branches that produce more than two leaves before conversion to flowering. The branches in *E. tenella* are similar to the lateral floral branches of the other species because they produce only one or two leaves and then a terminal flower. They differ from these branches because they do not die back after a flush of flowering; instead, they appear to continue producing one or two leaves (each with iterative axillary buds) and a terminal flower. Thus, the inflorescence in *E. tenella* is limited to the terminal flower produced by each axis. This alteration implies that whole plant architecture in *E. tenella* would differ significantly from the other species of the genus.

Among the species of sect. *Eucnide*, *E. cordata* has the most divergent inflorescence architecture because its penultimate internodes are distinctly elongated, as are those of the lateral floral branches. Waterfall (1959) noted this distinct architectural pattern in *E. cordata* and characterized the inflorescence as "lifted above the leaves on a short peduncle." He considered this to be the greatest tendency toward a terminal inflorescence in the genus.

Eucnide aurea and *E. cordata* may invest more heavily in flowers than other species. Both have a number of flowers that approach maturity simultaneously on inflorescence systems with extensive internodal elongation. In other species, floral buds remain small and inflorescence internodes are unextended until a particular flower begins to mature. *Eucnide cordata* and *E. aurea*, along with *E. rupestris* (the development of which I have not examined), are the only species that Thompson and Ernst (1967) reported to have many, crowded flowers in their inflorescences. These three species and *E. tenella* are primarily centered in Baja California, whereas the other *Eucnide* species are distributed throughout mainland Mexico and southwestern United States. Whether these similarities among species distributed in Baja California represent common ecological adaptations, phylogenetic constraints, or merely coincidental convergences should be investigated further. I have shown previously

(Hufford 1986) that individual flowers of *E. aurea* tend to be longer-lived following anthesis than flowers of other species of *Eucnide* (the same species as grown in glasshouse populations) that were investigated for this study. The persistence of individual flowers also may make this species appear to have many flowers that mature simultaneously.

The displaced terminal flowers of *E. urens* appear to be an extreme modification of the slight concaulescence that was observed commonly among the other species. *Eucnide urens* also differs from the other species because the leaf subtending a terminal flower is clasping. Waterfall (1959) noted that the "uppermost leaves [were] sometimes sessile and slightly amplexicaul". In the other species, leaves in the inflorescence region were often quite reduced, but they remained petiolate and were never clasping. These divergent features in the inflorescence region of *E. urens* support Thompson and Ernst's (1967) segregation of this species into its own section. Cladistic analysis of *Eucnide* (Hufford 1986) has shown that the *E. urens* complex is probably a sister group to the rest of the genus. The inflorescence features are among a suite of unique characteristics possessed by *E. urens* within the genus.

When Waterfall (1959) delineated two series in *Eucnide* based on inflorescence positions (the first series had solitary flowers in leaf axils and the second series had terminal inflorescences), he noted, "collections from young plants beginning to flower might be confused with the first group" (i.e., those thought to have solitary flowers in leaf axils). This observation is likely to be true because Waterfall and Thompson and Ernst (1967) each characterized at least some of the species as possessing axillary flowers. Axillary flowers have not been present in any of the material I examined. It is likely that the analyses presented in these systematic revisions were confused by the condensed internodes in the flowering region, the extended developmental period of the lateral floral branches, and the recaulescence in the floral branches. An accurate analysis of the inflorescence pattern in *Eucnide* would have been difficult without observation of the growth patterns of living plants. It is exceptionally difficult to determine inflorescence and branching patterns from herbarium specimens. Further comparative studies of 1) the developmental origin of the recaulescence common to most or all of the species, 2) the elongated internodes associated with the inflorescence region of *E. cordata*, and 3) the displacement of terminal flowers of *E. urens* are warranted.

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